Article (refereed) - postprint

Ward, Susan; Ostle, Nicholas J.; Oakley, Simon; Quirk, Helen; Henrys, Peter A.; Bardgett, Richard D.. 2013. **Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition.** *Ecology Letters*, 16 (10). 1285-1293. https://doi.org/10.1111/ele.12167

Warming effects on greenhouse gas fluxes in peatlands are modulated by vegetation composition

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Running title: Plants modulate warming effects on GHG fluxes

Keywords

Warming, greenhouse gas, plant functional group, plant community composition, peatland, CO_2, CH_4, N_2O, carbon cycle

24

25 Article type: Letter

26

27 Word count:

28 Abstract: 149 words

29 Main text: 4496 words

30 Text box: n/a

31

32 Number of references: 45

33 Number of Figures: 4

34 Number of Tables: 2

35 Number of text boxes: 0

36

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41 RDB and NJO conceived and designed the experiment, with input into the design from SEW.

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44 contributed with discussions and text.

45

ABSTRACT

Understanding the effects of warming on greenhouse gas feedbacks to climate change represents a major global challenge. Most research has focused on direct effects of warming, without considering how concurrent changes in plant communities may alter such effects. Here, we combined vegetation manipulations with warming to investigate their interactive effects on greenhouse gas emissions from peatland. We found that although warming consistently increased respiration, the effect on net ecosystem CO_2 exchange depended on vegetation composition. The greatest increase in CO_2 sink strength after warming was when shrubs were present, and the greatest decrease when graminoids were present. CH_4 was more strongly controlled by vegetation composition than by warming, with largest emissions from graminoid communities. Our results show that plant community composition is a significant modulator of greenhouse gas emissions and their response to warming, and suggest that vegetation change could alter peatland carbon sink strength under future climate change.

INTRODUCTION

There is growing concern about how biosphere carbon dynamics will respond to expected climate change, with evidence suggesting that atmospheric warming will increase soil respiration and greenhouse gas feedbacks (Bardgett *et al.* 2008; Craine *et al.* 2010). At the same time, terrestrial ecosystems are being subjected to increasing environmental pressures and human demands that are affecting vegetation community composition and diversity globally (Thuiller *et al.* 2005; Stevens *et al.* 2010). Despite widespread recognition that both climate and vegetation change can act independently as drivers of ecosystem carbon dynamics (De Deyn *et al.* 2008; Dorrepaal *et al.* 2009), we know little about the potential role in the carbon cycle of interactions between them (Bardgett *et al.* 2013). Indeed, experiments that explore the independent and interactive effects of abiotic and biotic factors as controls over ecosystem functioning are few (Hooper *et al.* 2005; Kardol *et al.* 2010), despite the suggestion that the magnitude of effects of vegetation change on ecosystem processes can be comparable to that of environmental change (Hooper *et al.* 2012; Tilman *et al.* 2012).

Carbon rich peatlands provide an ideal model system in which to examine the influence of warming and vegetation change on ecosystem greenhouse gas emissions; they have a relatively simple plant community structure, are recognised as important global sinks and sources of the greenhouse gases CO_2 and CH_4 respectively, and are vulnerable to land use and climate change (Dise 2009). Climate change models predict that northern latitude peatlands will be subjected to higher temperatures with longer growing seasons (IPCC 2007), and that this change will be accompanied by an increase in vascular plants at the expense of bryophytes and lichens (Walker *et al.* 2006; Gallego-Sala & Prentice 2013). Recent work has shown that experimental warming can significantly increase rates of peatland ecosystem respiration (Dorrepaal *et al.* 2009; Briones *et al.* 2010), and that drought can induce carbon

loss *via* changes in soil enzyme activity (Fenner & Freeman 2011). Other peatland studies suggest that there are key differences in the ecophysiological traits of dominant plant functional groups, that have a strong regulatory role in ecosystem carbon dynamics (Ward *et al.* 2012). Despite this, it is not known whether changes in plant community structure, and the presence or absence of dominant peatland plant functional groups (*i.e.*, shrubs, graminoids and bryophytes), will modify the impact of warming on ecosystem greenhouse gas fluxes. This represents a serious knowledge gap, given that most plant communities globally are subject to both vegetation and climate change, but their combined impact on greenhouse gas fluxes is not known.

To redress this gap in knowledge, we established a unique field experiment in spring 2008 with the aim of examining the independent and interactive effects of warming and plant functional composition on greenhouse gas exchange in a peatland ecosystem. We used a plant removal approach to manipulate vegetation composition (Diaz *et al.* 2003; Wardle & Zackrisson 2005) from an area of ombrotrophic blanket bog in northern England. Vegetation manipulations included removal of all possible combinations of the three dominant plant functional groups, namely ericoid shrubs, graminoids (sedges), and bryophytes/lichens. Warming was induced passively on half of the experimental plots, using randomly allocated hexagonal open-top chambers (OTCs) (Marion *et al.* 1997) which increased air temperatures by approximately 1°C over the mid-day period. We present results from field measurements of greenhouse gas fluxes, namely net ecosystem exchange (NEE) of CO_2, ecosystem respiration, CH_4 and N_2O fluxes for all times of year spanning two growing seasons. We show that, although rates of ecosystem respiration were consistently increased by warming across all vegetation types, the effect of warming on NEE, once differences in photosynthetic uptake of CO_2 were taken into account, was dependent on plant community composition.

More specifically, the greatest increase in CO_2 sink strength after warming was observed when shrubs only (dominated by *Calluna vulgaris*) were present. Also, warming reduced mean CO_2 sink strength in the presence of graminoids, and increased CO_2 sink strength when graminoids were absent. In addition, we found that the efflux of CH_4 was more strongly controlled by plant community composition than by warming, with largest emissions coming from sedge (*Eriophorum vaginatum*) dominated communities. Taken together, these findings highlight the importance of plant community composition as a driver of carbon cycling processes, and show that plant community composition can modulate the effects of warming on net ecosystem exchange of CO_2.

MATERIALS AND METHODS

Study site.

The study site was situated on an area of ombrotrophic blanket bog within the Moor House National Nature Reserve in northern England (54°65' N, 2°45' W). The site altitude was 550m, the mean annual temperature is 5.8°C, and the mean annual precipitation 2048mm (UK Environmental Change Network, www.data.ecn.ac.uk). The mean depth of peat at the site was 1.17m (± 0.01), and the mean pH 4.07 (± 0.01). Abiotic conditions, including air and soil temperature, solar radiation, photosynthetically active radiation and rainfall at the site were recorded by the Moor House automated weather station (www.ecn.ac.uk) (Supporting information, Table S1).

Vegetation manipulation and climate warming.

Vegetation removals were undertaken by hand, from areas measuring 1.5 x 1.5m, separated by a buffer zone of at least 1m from adjoining plant removal plots. Shoots of shrubs and graminoids were cut back to litter layer level, and all green (photosynthetic) tissues of bryophytes were removed, taking care to minimise disturbance of the soil and remaining vegetation types. Wooden boardwalks were installed on two sides of each removal plot, to allow access to the sampling plots without damage by trampling. Plots were left to settle for a year before sampling to minimise effects of decomposition from roots. The use of this plant removal approach allowed us to measure the effects of plant functional groups *in situ* in their natural environment (Diaz *et al.* 2003). The plant functional group manipulations were from the three dominant vegetation types present: ericoid dwarf-shrubs (S), dominated by *Calluna vulgaris* (L.) Hull*;* graminoids (G), dominated by the sedge *Eriophorum vaginatum* L*;* and bryophytes/lichens (B) dominated by feather mosses (*Hypnum jutlandicum* Holm. &

Warncke; *Pleurozium schreberi* (Brid.) Mitt.) and *Sphagnum* mosses. There were 8 different plant manipulations: a control with all vegetation present, three single groups (S, G or B), three double groups (S&G, S&B, G&B) and a treatment where all above ground vegetation was removed. The experiment site had four blocks, containing randomly arranged warmed and non-warmed replicates of each plant manipulation treatment (n = 64).

Warming was achieved passively using hexagonal OTCs based on the ITEX design (Marion *et al.* 1997), modified for peatland vegetation by the addition of a 20cm high vertical galvanised steel base, on to which the transparent top sections were fixed using cable ties. Each transparent section making up the hexagonal OTC measured 80cm along the bottom edge, 62.5cm along the top edge and 40cm height, to give an internal diameter of $1m^2$, avoiding edge effects. The transparent material was 2mm thick Liteglaze clear acrylic sheet (Ariel plastics, UK), which allows 92% light transmission. The open-topped chamber method offers a robust means to examine effects of warming in remote environments, without the need for a power supply, and has been used frequently in arctic and peatland ecosystems (Walker *et al.* 2006; Dorrepaal *et al.* 2009). This methodology has its limitations, most notably that OTCs can act as a physical barrier to wind (Marion *et al.* 1997), which, in addition to changing temperature, has the potential to alter the width of the boundary layer and hence the concentration of CO_2 surrounding photosynthesising leaves, thereby affecting rates of photosynthetic uptake of carbon. Despite these limitations, the technique provides a valid and useful way of quantitatively comparing the effects of warming between experimental vegetation removal treatments in the field.

The OTCs were fixed in place one month prior to commencement of sampling. Air temperatures at vegetation canopy height were recorded using temperature loggers (Lascar

Electronics, Salisbury, UK). Water table levels were measured from dip-wells made of 1m long perforated PVC pipe, installed in each of the 64 experimental plots. On average, the OTC's increased mean air temperatures by 0.88°C and 0.72°C over the midday period (during the gas sampling period between 11:00 and 14:00 hrs), for the growing and non-growing season respectively. Over 24 hours, the mean increase in temperature was 0.46°C and 0.21°C for the growing and non-growing seasons. We found no evidence of any difference in water table draw-down due to warming ($F_{1,1476} = 0.2$, $P = 0.87$), or due to vegetation type ($F_{1,1476} = 0.9$, $P = 0.33$). For full details of the abiotic conditions during all sampling dates, see Table S1.

Greenhouse gas flux measurements.

In each sampling plot, a 30 cm diameter, 10cm high gas sampling base ring was fitted in place at 5cm depth, with care taken to minimise disturbance and to avoid severance of large plant roots. Boardwalks installed on two sides of each experimental plot allowed access to the sampling areas without compressing the surrounding peat, which could have created physical movement of gases. Measurements of CO_2 exchange were made over 120-s intervals with a PP systems EGM4 portable IRGA coupled to a customised chamber lid, 30cm diameter and 35cm height (Ward *et al.* 2007). We used the dark and light flux method for ecosystem respiration and net CO_2 flux respectively (Ward *et al.* 2007). Measurements were taken between 11:00 and 14:00 hours from June 2009 to August 2010, at approximately monthly intervals during the growing season, and bi-monthly at other times. For CH_4 and N_2O, bi-monthly gas samples were collected on closure of the chamber lid and at three additional time points up to 30 minutes closure. Gas samples (10ml) were taken from the chamber headspace using a gas syringe, and injected into evacuated 3ml exetainers (Labco, UK) for storage prior to analysis. Concentrations of CH_4 and N_2O were analysed by gas

chromatography, using Perkin Elmer Autosystem XL GCs with a flame ionisation detector for CH_4 and electron capture detector for N_2O. GC detection limits were better than 0.2 ppm for all gases. For each sample, 2.5ml of gas was injected into the GC using an HTA Autosampler. Results were calibrated against certified gas standards, comprising 500ppm CO_2, 10ppm CH_4 and 1ppm N_2O (BOC, UK). All fluxes were adjusted for field sampling temperature, headspace volume and chamber area (Holland *et al.* 1999), and calculated by linear regression using all time points sampled (Levy *et al.* 2012).

Soil properties

Peat cores measuring 3cm diameter and 10cm depth were collected from each field plot in July of the final year of gas sampling, in order to gain a measure of microbial biomass and the availability of dissolved organic carbon (DOC) and nitrogen (DON) in the peat. Peat was homogenised and hand sorted to remove any root material, then analysed for microbial biomass C and N using fumigation-extraction, and water extractable DOC and DON using methods described in Ward *et al.* (2007).

Statistics.

Data were checked for normality using residual plots method, and log-transformed where necessary before analysis. The effects of experimental warming and vegetation manipulations, and their interactions, were analysed by repeated measures ANOVA, using SAS Enterprise Guide 4, with sampling date nested within sampling block as random effects. Vegetation effects were analysed as the presence and absence of each of the three plant functional groups (shrubs, graminoids and bryophytes), and effects of vegetation diversity were analysed based on the number of plant functional groups present. After confirming a three way interaction between season, warming and plant functional group, data were

220 analysed as 2 separate models: 1) growing season data; and 2) non growing season data, with
221 growing season defined as when the mean air temperature is greater than 6ºC.
222

RESULTS

CO_2

Our results show that the effect of warming on NEE of CO_2 was modulated by the removal of different plant functional groups in the experimental communities (Fig 1, Table 1). A significant interaction ($F_{1,744} = 6.4$, $P = 0.0126$) between warming and plant functional group removal on NEE was observed during the growing season (*i.e.* when average air temperature was > 6°C). More specifically, mean CO_2 sink strength increased by 55% with warming in plots where shrubs were the only plant functional group present, and by 36% when shrubs were present with bryophytes, but without graminoids (Fig. 1). In the presence of graminoids, however, mean CO_2 sink strength was reduced by 20% with warming, whereas in the absence of graminoids, mean CO_2 sink strength was increased by 43% with warming. Vegetation diversity also influenced NEE ($F_{3,744} = 18.3$, $P < 0.0001$), with strongest effects seen when comparing non-vegetated plots with those containing 2 or 3 plant functional groups, but there were no interactions between vegetation diversity and warming (Supporting information, Table S2).

Ecosystem respiration rates were consistently raised by warming across all vegetation treatments (Fig. 2), but there were no detectable interactions of warming with the removal of shrubs, graminoids or bryophytes (Table 1). Across all vegetation removal treatments, warming of ~1°C over the year increased rates of ecosystem respiration in warmed relative to non-warmed treatment plots by a mean of 47% and 49%, during the growing and non-growing seasons respectively ($F_{1,734} = 49.8$, $P < 0.0001$; $F_{1,227} = 10.1$, $P = 0.002$). There were also highly significant effects of shrub, graminoid, and bryophyte removal on ecosystem respiration rates, with strongest effects during the growing season, and interactions observed between graminoids and the other plant functional groups (Table 1). The highest rates of

248 respiration were measured in the presence of vascular plants, and there was a greater
249 reduction in respiration from the removal of shrubs than from the removal of graminoids.
250 When bryophytes were removed, rates of respiration increased, however this effect was only
251 observed during the growing season (Table 1). Significantly lower rates of respiration were
252 measured for bare plots compared to those with one or more plant functional group present
253 ($F_{3,734}$ = 21.1, P < 0.0001), but there was no interaction of vegetation diversity with warming
254 (Supporting information, Table S2).
255
256 **CH_4 and N_2O**
257 We found that vegetation composition, particularly the presence of graminoids, was a
258 stronger factor than warming in regulating peatland CH_4 fluxes (Fig. 3, Table 1), and that the
259 presence and absence of graminoids and shrubs interacted to affect net CH_4 exchange all year
260 round. Emissions of CH_4 were higher in the presence relative to absence of graminoids, but
261 lower in the presence relative to absence of shrubs. We measured the highest CH_4 fluxes
262 when graminoids (the sedge, *Eriophorum vaginatum*) were present without shrubs and
263 without bryophytes (Fig. 3). Warming effects on CH_4 efflux were only significant during the
264 growing season ($F_{1,251}$ = 5.6, P = 0.02), but we detected no interactive effect of warming with
265 vegetation removal on ecosystem CH_4 emissions for any of the three plant functional groups
266 (Table 1). Outside the growing season, the peatland was seen to be a small sink for CH_4 in
267 the absence of vegetation, and when shrubs and bryophytes only were present in warmed
268 plots (Fig. 3).
269
270 For N_2O, we found no significant effect of warming either during ($F_{1,167}$ = 0.0, P = 0.92) or
271 outside the growing season ($F_{1,167}$ = 2.5, P = 0.12), although there was a trend for a greater
272 N_2O sink in warmed plots during the non-growing season (Fig. 4, Table 1). During the

growing season we detected an interactive effect between shrubs and bryophytes, whereby the greatest mean sink for N_2O was measured when shrubs were present and bryophytes had been removed. There were no interactions between warming and vegetation removal, and no significant effect of plant diversity on N_2O flux.

Soil properties

Warming increased concentrations of DOC ($F_{1,64}$ = 6.1, P = 0.02) and DON ($F_{1,64}$ = 7.0, P = 0.01) in soil solution by 13% and 15% respectively (Table 2). Vegetation change was found to have a stronger effect on DOC and DON than warming, with the removal of shrubs increasing concentrations of DOC ($F_{1,64}$ = 22.4, P < 0.0001) and DON ($F_{1,64}$ = 21.0, P < 0.0001) by 21%. In contrast, the graminoid or bryophyte removal had no detectable effect on DOC or DON, and no interactions between warming and vegetation change were detected (Supporting information, Table S3). Microbial biomass C and N did not respond to warming, although microbial N was affected by vegetation change: microbial biomass N was greatest when both shrubs and bryophytes were removed (Supporting information, Table S3), and microbial C:N ratio was 14% lower when shrubs were removed ($F_{1,64}$ = 5.4, P = 0.02).

DISCUSSION

It has long been recognised that carbon cycling processes in peatlands are highly sensitive to changes in climate (Dise 2009; Dorrepaal *et al.* 2009), and there is growing evidence that climate driven vegetation change in peatland and high latitude ecosystems is leading to an increase in vascular plants at the expense of bryophytes (Walker *et al.* 2006; Gallego-Sala & Prentice 2013). However, despite these concurrent changes in climate and vegetation, their interactive effects on greenhouse gas fluxes are virtually unknown. We, therefore, set out to examine the independent and interactive effects of warming and plant functional composition on greenhouse gas exchange in a peatland ecosystem, using a unique field plant manipulation and warming experiment. Our findings provide the first evidence that the response of peatland greenhouse gas exchange to warming is both modulated and strongly controlled by plant community composition.

Our results show that removal of different plant functional groups in the experimental communities modulated the effects of warming on NEE of CO_2. In particular, we found that, during the growing season, a significantly greater increase in net CO_2 sink strength with warming was seen in the presence of shrubs when graminoids were absent, whereas warming had the opposite effect in the presence of graminoids. As the main terrestrial exchange of carbon from peatlands is as CO_2 (Roulet *et al.* 2007), quantifying NEE of CO_2 allows us to get a measure of the net ecosystem carbon balance of the system, and how this is affected by warming and vegetation community composition. The clear interactive effect of warming and plant functional group removal on NEE during the growing season (*i.e.* when average air temperature was > 6°C), suggests that responses were dependent on feedbacks from actively growing plants, supporting the idea that the composition of actively growing peatland vegetation is a key modulator of the response of ecosystem CO_2 fluxes to climate change. In

contrast, although ecosystem respiration rates were consistently raised by warming across all vegetation treatments, no such interaction of warming with vegetation composition was detected. Given the similarity of the respiration responses of different plant functional groups to warming, we propose that observed differences in NEE are largely attributable to differences in photosynthetic CO_2 uptake, with shrubs growing alone, or shrubs with bryophytes, showing the greatest increase in photosynthesis relative to respiration and hence, increased net CO_2 sink strength, with warming. In contrast, in the presence of graminoids, warming led to a greater increase in rates of respiration relative to photosynthesis, leading to a reduction in net CO_2 sink strength. Differences in rates of assimilation of CO_2 and translocation of new photosynthates below-ground have previously been observed among dominant peatland plant functional groups (Ward *et al.* 2012), with vascular plants (shrubs and graminoids) showing greater rates of CO_2 assimilation and transfer relative to bryophytes. This significant positive effect of warming on photosynthetic drawdown of CO_2 by shrubs is likely to be a consequence of their characteristic ecophysiological traits related to resource acquisition, including associations with ericoid mycorrhizal fungi (Read *et al.* 2004), and canopy height and bushy growth habit, which makes them better placed to intercept light and to shade vegetation beneath their canopy.

Another explanation for the differences in warming response of NEE across plant functional groups might be associated shifts in microbial communities in the peat, which could ultimately affect the balance between CO_2 uptake and release under warming (Bardgett *et al.* 2008). It is known that shrubs and graminoids in peatlands differ in the rate that they allocate photosynthetic carbon below-ground (Ward *et al.* 2009; Ward *et al.* 2012), and such differences in allocation are likely to affect the quality and quantity of exudates released from roots, to mycorrhizal fungi, and ultimately to soil, thereby affecting the composition and

activity of microbial communities (De Deyn *et al.* 2008; Bardgett *et al.* 2013). Also, observed differences in the photosynthetic response of plant functional groups to warming are likely to have altered carbon flux to roots and rates of root exudation, thereby further contributing to shifts in the composition and activity of microbial communities across vegetation treatments, and potentially explaining differential responses of NEE to warming. We did not measure soil microbial community structure in this study, but we did find, albeit at one sample date, that microbial C:N was significantly affected by shrub removal, which could be indicative of a change in microbial communities. This is perhaps due to the high concentrations of phenolic compounds (Hattenschwiler & Vitousek 2000; Freeman *et al.* 2001) and the presence of mycorrhizal fungi (Read *et al.* 2004; Orwin *et al.* 2011) associated with ericoid shrubs. More studies are clearly needed to unravel the mechanisms by which differences in vegetation modulate responses of NEE to warming, including studies on the potential role of shifts in microbial communities as determinants of the response of NEE to warming.

The mean increase in rates of ecosystem respiration in response to ~1°C warming, of 47-49%, is consistent with other studies of warming effects in peatlands, observed in the field (Dorrepaal *et al.* 2009) and laboratory (Kim *et al.* 2012). As with our findings for NEE of CO_2, the greatest effects of vegetation composition were observed during the growing season, with the highest respiration rates being measured when vascular plants (*i.e.*, shrubs and graminoids) were present in the plant community. We also observed warming effects on concentrations of DOC and DON in soil solution, which were found to be higher in soils from the warmed than unwarmed plots at the peak of the growing season, which is likely indicative of an increase in microbial activity in response to warming. Although the effects of warming and vegetation composition on ecosystem respiration were found to be

365 independent, our findings do highlight the importance of both warming and actively growing
366 vegetation in controlling the release of CO_2 to the atmosphere by respiration.
367
368 Peatlands are a globally important source of CH_4 (Baird *et al.* 2009) and previous work has
369 shown that both warming (van Winden *et al.* 2012) and vegetation (Levy *et al.* 2012; Gray *et*
370 *al.* 2013) can have a measureable effects on ecosystem CH_4 emissions. Our study provides
371 the first *in situ* field experimental evidence that vegetation composition is a stronger factor
372 than ~ 1°C warming in regulating peatland CH_4 fluxes. As with our findings for CO_2, the
373 effects of vegetation community composition were stronger during the growing season than
374 for the rest of the year, which again, highlights the key role that actively growing vegetation
375 can play in controlling GHG exchange. The relatively greater levels of CH_4 efflux when the
376 graminoid *Eriophorum vaginatum* was present, may be explained by the recognised
377 functional traits of this wetland sedge, namely the presence of aerenchymous tissues which
378 act as a conduit for CH_4 from the catotelm (Strack *et al.* 2006; Green & Baird 2012). In
379 addition, differences in the quality and quantity of root exudates entering the soil from
380 contrasting plant functional groups (De Deyn *et al.* 2008) are likely to affect the activity of
381 methanogenic bacteria in the peat, as well as respiration processes. Sedges in particular have
382 been associated with enhanced CH_4 production due to an increased supply of available
383 substrates, particularly acetate, to methanogens (Bellisario *et al.* 1999; Hornibrook 2009; Lai
384 2009), providing an additional explanation for the increased CH_4 emissions we observed in
385 the presence of graminoids. Interestingly, we observed that the system was a small sink for
386 CH_4 in the absence of vegetation, and also when shrubs and bryophytes only were present in
387 warmed plots outside the growing season. This implies that, even out of the growing season,
388 the presence of vegetation is still exerting controls on CH_4 emissions, through either changes
389 in microbial activity, or differences in physical conditions. Although peatlands are associated

with greater CH_4 productivity than consumption, there is some evidence of CH_4 consumption in peat, particularly by methylocystis-related species (Kolb & Horn 2012).

Whereas previous peatland observations of high CH_4 emissions from sedge dominated communities come from contrasting physical habitats (Strack *et al.* 2006; McNamara *et al.* 2008), our plant manipulation approach allowed us to compare plant functional groups in the same habitat, providing new evidence of the importance of vegetation composition in controlling CH_4 emissions. Although warming did increase the mean CH_4 efflux for all vegetation manipulation treatments by 90% during the growing season, these effects were much weaker than those observed due to vegetation composition, and we found no statistical evidence that warming effects differed between vegetation types.

Atmospheric exchange of N_2O, the third greenhouse gas measured in this study, was relatively low, as would be expected in nutrient poor ecosystems such as peatlands (Reay *et al.* 2012). These small fluxes, which varied between net emissions and net uptake (Fig. 4), are typical of northern ombrotrophic peatlands (Drewer *et al.* 2010). Despite this, vegetation composition was found to impact on sink strength for N_2O during the growing season, being greatest when shrubs were present and bryophytes had been removed. Unlike for other greenhouse gases, however, we detected no response of warming on N_2O, aside a weak increase in N_2O sink strength, suggesting that climate warming is unlikely to affect the atmospheric exchange of N_2O in peatland in this N poor blanket peatland. In contrast, studies of N_2O emissions from peatlands which are more nutrient-rich (Martikainen *et al.* 1993), or which have patches of bare soil with high nitrate content due to cryoturbation (Repo *et al.* 2009), have shown that climate warming can have powerful effects on peat N_2O fluxes.

In conclusion, our findings provide evidence from a unique field manipulation experiment that warming effects on greenhouse gas exchange in peatland are modulated by changes in plant community composition, with the greatest increase in net CO_2 sink strength with warming occurring when shrubs were present and graminoids were absent. A change in the rate of greenhouse gas exchange with the atmosphere, brought about by increased domination by vascular plants as peatlands warm, has the potential to feedback to global climate change by exacerbating radiative forcing. Furthermore, the observed interaction of climate warming with vegetation change could accelerate these feedbacks in peatland systems containing large stocks of globally important carbon (Gallego-Sala & Prentice 2013). Whilst the mechanisms that underlie our findings require further exploration, our results indicate that changes in vegetation community composition can act as a strong determinant of climate change effects on northern peatland carbon cycling. As such, these results highlight the importance of considering biotic as well as abiotic climate induced changes when predicting the future greenhouse gas sink/source strength of peatland ecosystems.

ACKNOWLEDGEMENTS

This research was supported by a Natural Environment Research Council (NERC) EHFI grant (NE/E011594/1) awarded to R D Bardgett, as lead investigator, and N J Ostle. We thank colleagues from CEH Lancaster and Lancaster University for help in the field. We also thank Natural England and the Environmental Change Network, CEH Lancaster, for site access and weather station data. We are grateful to three anonymous referees for their valuable comments on an earlier version of this manuscript.

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606

607 **SUPPORTING INFORMATION**

608 Additional supporting information may be downloaded via the online version of this article at
609 Wiley Online Library (www.ecologyletters.com).

610 **Table S1**. Abiotic conditions for all sampling dates.

611 **Table S2.** Effects of vegetation diversity on CO_2, CH_4 and N_2O.

612 **Table S3.** Statistical analysis for DOC, DON and microbial biomass C and N.

613

TABLES

Table 1. Statistical analysis for the effects of, and interactions between, warming and the presence/absence of plant functional groups on CO_2, CH_4 and N_2O fluxes by seasons: a) growing season May to September, b) non-growing season October to April.

619 Table 1

Source of variation	a) Growing season (May – Sept)			b) Non-growing season (Oct – April)		
	df	f	p	df	f	p
Net ecosystem CO_2 exchange ***(mg m^{-2} h^{-1})***			(n = 744)			(n = 229)
Warming	1	0.0	0.86	1	3.1	0.08
Shrub presence/absence	1	151.4	<0.0001	1	21.1	<0.0001
Graminoid presence/absence	1	17.1	<0.0001	1	2.8	0.10
Bryophyte presence/absence	1	0.1	0.82	1	1.6	0.21
Warmed x shrub	1	0.5	0.48	1	2.5	0.12
Warmed x graminoid	1	8.0	0.005	1	0.0	0.97
Warmed x bryophyte	1	0.4	0.52	1	1.5	0.22
Shrub x graminoid	1	13.4	0.0004	1	0.0	0.95
Shrub x bryophyte	1	2.7	0.10	1	1.7	0.20
Graminoid x bryophyte	1	2.9	0.09	1	1.9	0.18
Warmed x shrub x graminoid	1	6.4	0.01	1	0.1	0.81
Warmed x shrub x bryophyte	1	0.0	0.87	1	1.4	0.25
Warmed x graminoid x bryophyte	1	0.2	0.67	1	0.1	0.77
Ecosystem respiration ***(mg m^{-2} h^{-1})***			(n = 734)			(n = 227)
Warming	1	49.8	<0.0001	1	10.1	0.002
Shrub presence/absence	1	164.7	<0.0001	1	22.6	<0.0001
Graminoid presence/absence	1	32.8	<0.0001	1	6.1	0.016
Bryophyte presence/absence	1	5.4	0.022	1	0.4	0.55
Warmed x shrub	1	1.0	0.31	1	0.5	0.51
Warmed x graminoid	1	0.2	0.63	1	0.2	0.69
Warmed x bryophyte	1	0.5	0.50	1	0.1	0.72
Shrub x graminoid	1	14.3	0.0002	1	2.4	0.12
Shrub x bryophyte	1	0.0	0.90	1	1.3	0.26
Graminoid x bryophyte	1	19.3	<0.0001	1	2.0	0.16
(no significant 3 way interactions)						
CH_4 (mg m^{-2} h^{-1})			(n = 251)			(n = 218)
Warming	1	5.6	0.02	1	0.3	0.58
Shrub presence/absence	1	9.9	0.002	1	1.5	0.22
Graminoid presence/absence	1	10.1	0.002	1	15.9	0.0001
Bryophyte presence/absence	1	2.2	0.14	1	2.4	0.12
Warmed x shrub	1	0.1	0.78	1	2.8	0.10
Warmed x graminoid	1	0.4	0.55	1	0.6	0.44
Warmed x bryophyte	1	0.1	0.70	1	1.2	0.28
Shrub x graminoid	1	8.5	0.005	1	13.9	0.0003
Shrub x bryophyte	1	0.0	0.92	1	2.4	0.12
Graminoid x bryophyte	1	1.3	0.26	1	10.5	0.002
(no significant 3 way interactions)						
N_2O (mg m^{-2} hr^{-1})			(n = 164)			(n = 167)
Warming	1	0.0	0.92	1	2.5	0.12
Shrub presence/absence	1	0.1	0.82	1	0.5	0.50
Graminoid presence/absence	1	0.7	0.39	1	1.3	0.27
Bryophyte presence/absence	1	0.2	0.65	1	1.1	0.29
Warmed x shrub	1	0.1	0.76	1	2.2	0.14
Warmed x graminoid	1	1.1	0.31	1	0.2	0.63
Warmed x bryophyte	1	0.4	0.55	1	1.4	0.25
Shrub x graminoid	1	1.0	0.32	1	0.8	0.37
Shrub x bryophyte	1	4.2	0.04	1	0.4	0.51
Graminoid x bryophyte	1	0.1	0.71	1	0.2	0.63
(no significant 3 way interactions)						

620

621 **Table 2**. DOC and DON in soil solution, and microbial biomass C and N in soils, sampled
622 during the growing season. Values are means +/- s.e.

Vegetation type	**DOC** (µg C g dry wt soil^{-1})	**DON** (µg N g dry wt soil^{-1})	**Microbial Biomass C** (mg C g dry wt soil^{-1})	**Microbial Biomass N** (mg N g dry wt soil^{-1})
Non-warmed				
Control	1304 (± 188)	686 (± 99)	19.3 (± 2.7)	3.2 (± 0.2)
Shrub only	1514 (± 131)	814 (± 76)	11.8 (± 3.4)	2.6 (± 0.6)
Graminoid only	2135 (± 237)	1164 (± 199)	13.6 (± 2.6)	3.5 (± 0.6)
Bryophyte only	2115 (± 205)	1185 (± 128)	14.7 (± 2.6)	3.3 (± 0.5)
Shrub + Graminoid	1357 (± 179)	726 (± 86)	17.0 (± 1.3)	3.0 (± 0.2)
Shrub + Bryophyte	1928 (± 170)	1018 (± 79)	18.3 (± 2.2)	3.7 (± 0.5)
Graminoid + Bryophyte	2141 (± 161)	1128 (± 84)	13.5 (± 1.9)	2.5 (± 0.2)
No vegetation	2020 (± 306)	1065 (± 157)	16.8 (± 1.6)	3.4 (± 0.5)
Warmed				
Control	1901 (± 267)	1169 (± 235)	16.0 (± 0.9)	3.1 (± 0.2)
Shrub only	2331 (± 166)	1216 (± 98)	10.7 (± 1.9)	2.2 (± 0.7)
Graminoid only	2096 (± 149)	1108 (± 81)	11.7 (± 0.8)	3.0 (± 0.4)
Bryophyte only	1900 (± 56)	1026 (± 31)	9.2 (± 1.8)	2.1 (± 0.6)
Shrub + Graminoid	1722 (± 240)	951 (± 123)	16.8 (± 1.0)	3.0 (± 0.8)
Shrub + Bryophyte	1531 (± 104)	789 (± 51)	15.8 (± 3.2)	3.6 (± 1.3)
Graminoid + Bryophyte	2376 (± 134)	1302 (± 83)	17.2 (± 0.8)	3.7 (± 0.5)
No vegetation	2502 (± 336)	1363 (± 145)	13.7 (± 0.8)	3.6 (± 0.4)

623

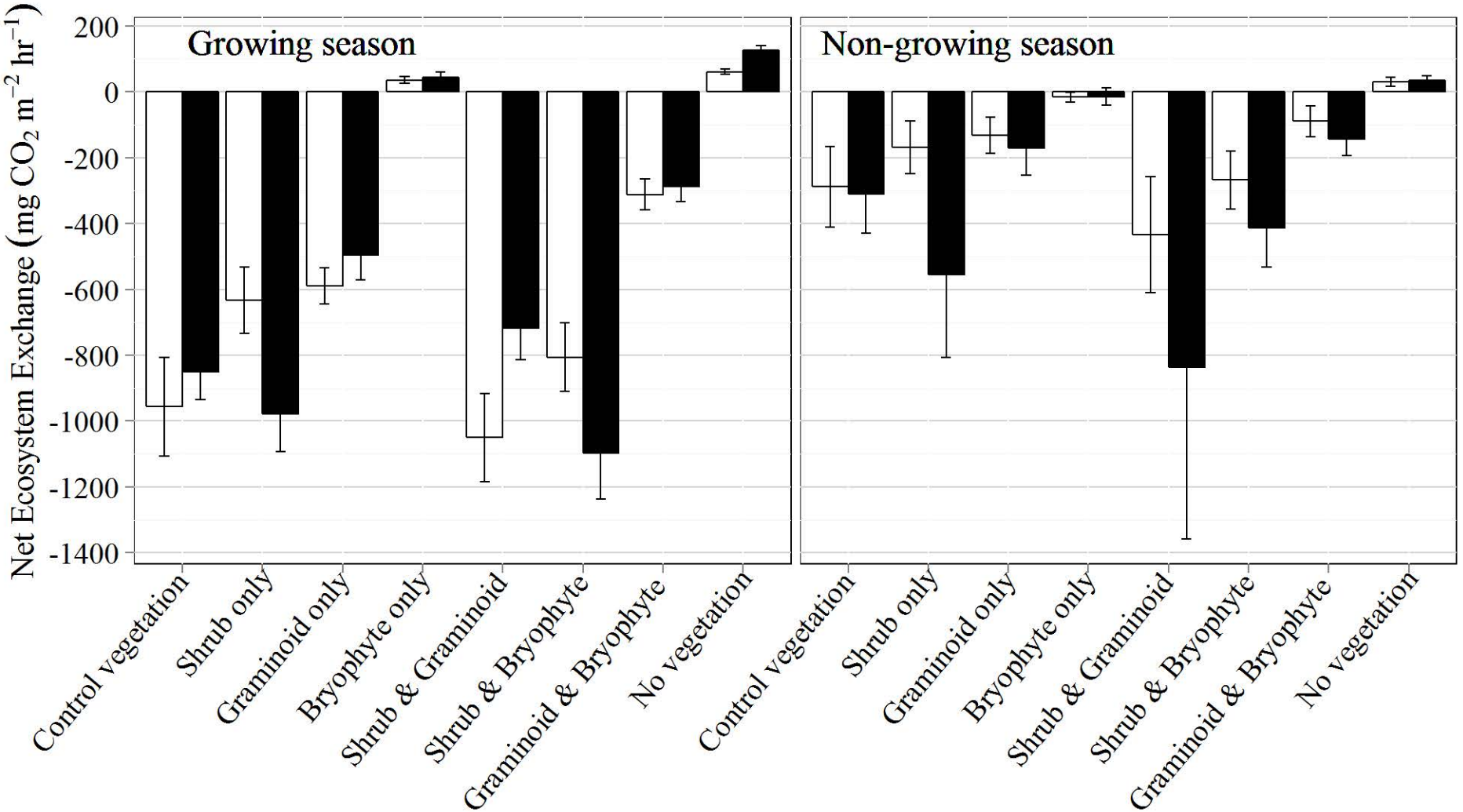
FIGURE LEGENDS

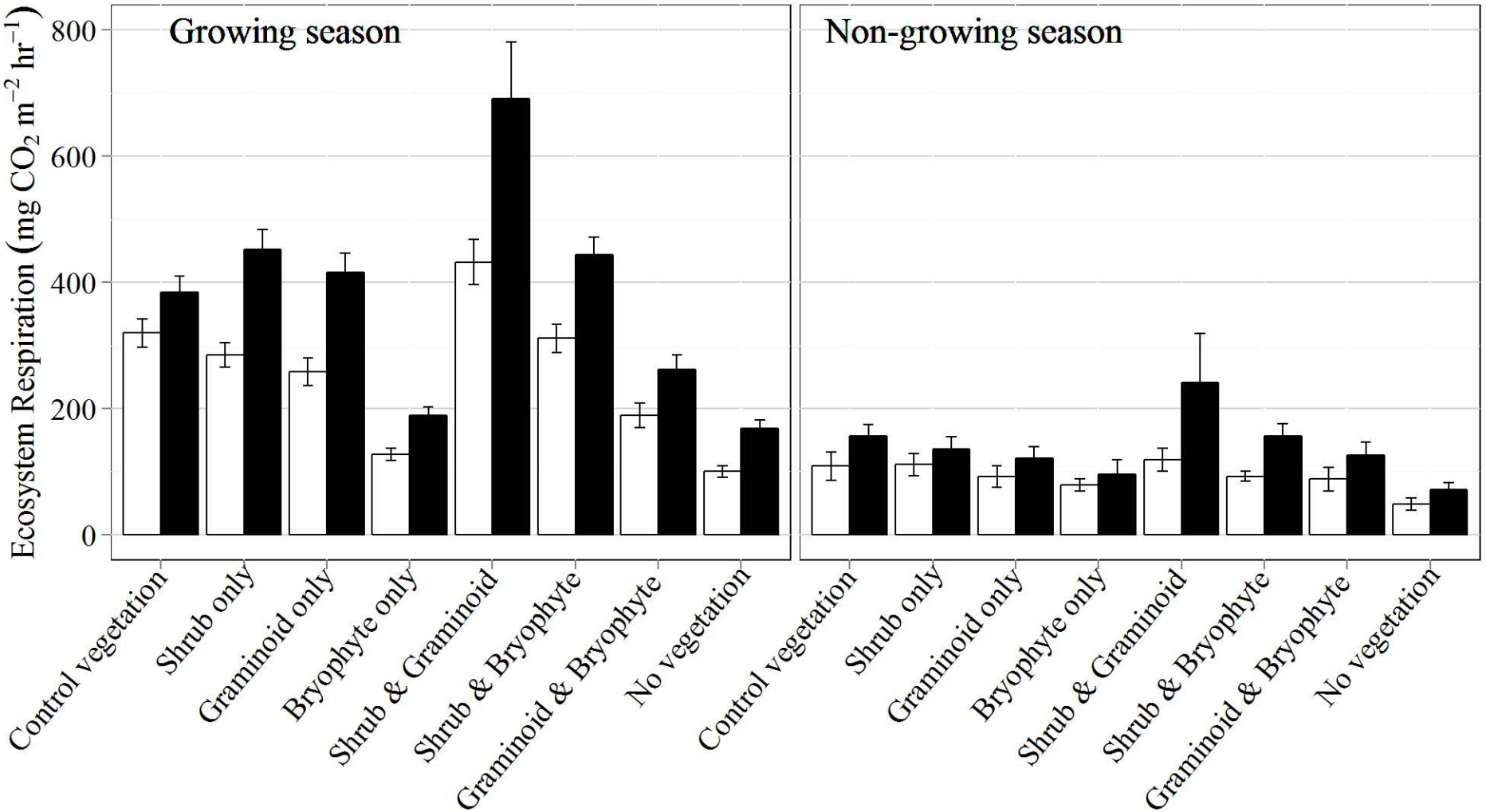
Figure 1. Net ecosystem CO_2 exchange from the plant manipulation and warming experiment. Data are means (mg CO_2 m^{-2} hr^{-1}) for all sampling dates +/- standard error. White bars are for non-warmed and black bars are for warmed experimental field plots. Data are split between: growing season of May to September (left), and non-growing season of October to April (right). Negative values respresent a net sink and positive values represent a net source for CO_2.

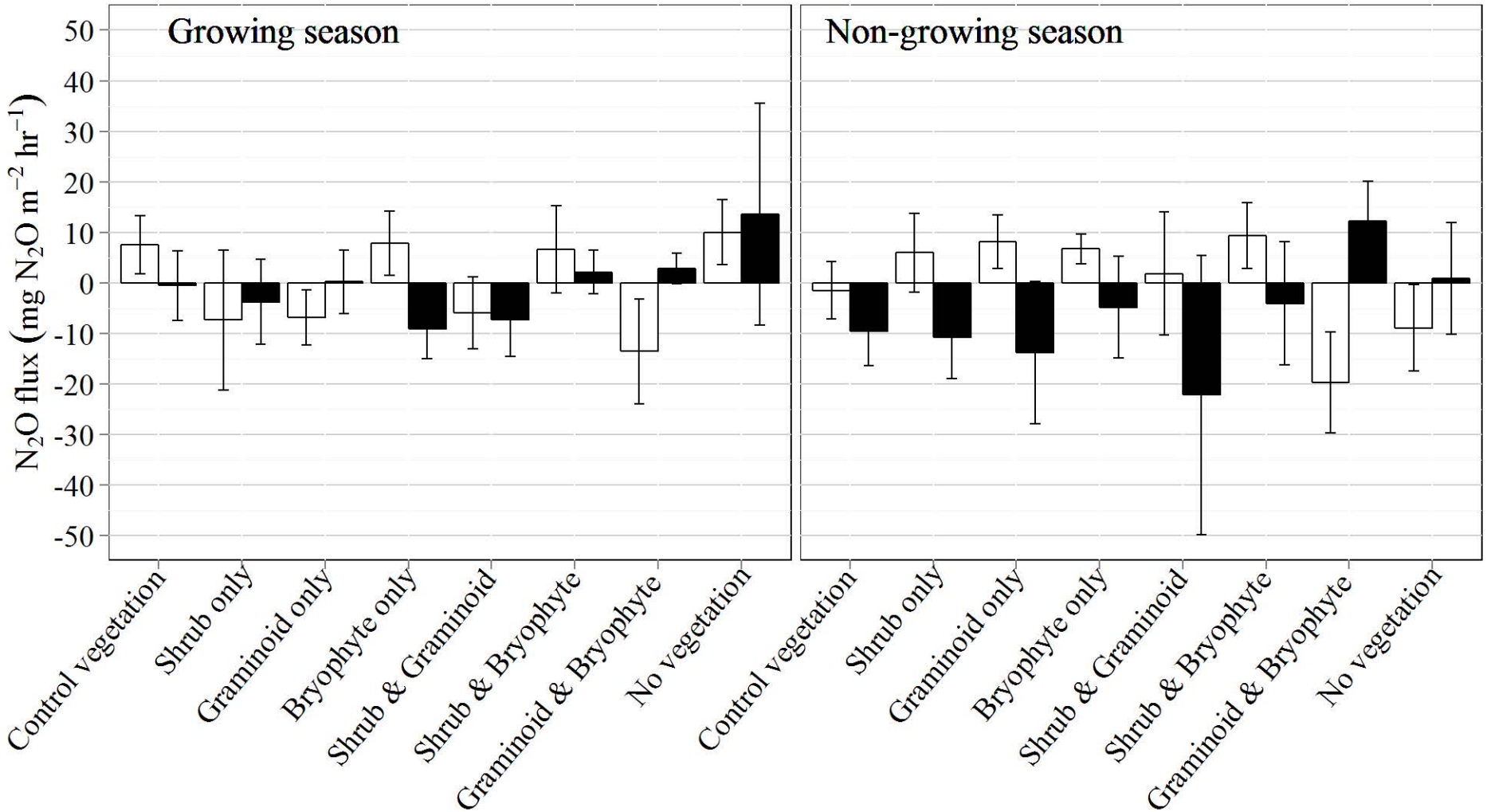
Figure 2. Ecosystem respiration from the plant manipulation and warming experiment. Data are means (mg CO_2 m^{-2} hr^{-1}) for all sampling dates +/- standard error. White bars are for non-warmed and black bars are for warmed experimental field plots. Data are split between: growing season of May to September (left), and non-growing season of October to April (right).

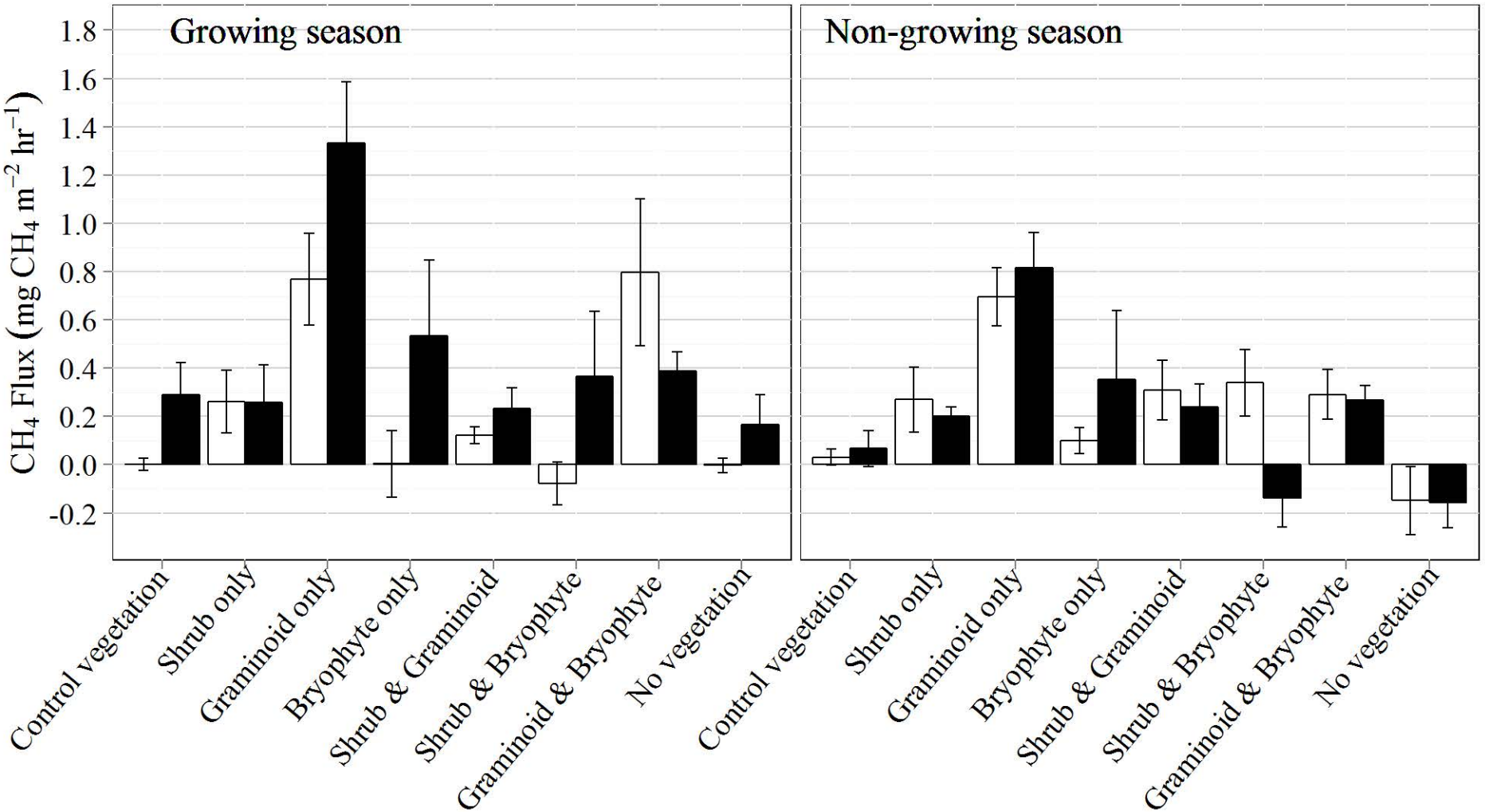
Figure 3. Methane flux from the plant manipulation and warming experiment. Data are means (mg CH_4 m^{-2} hr^{-1}) for all sampling dates +/- standard error. White bars are for non-warmed and black bars are for warmed experimental field plots. Data are split between: growing season of May to September (left), and non-growing season of October to April (right).

Figure 4. Nitrous oxide flux from the plant manipulation and warming experiment. Data are means (mg N_2O m^{-2} hr^{-1}) for all sampling dates +/- standard error. White bars are for non-warmed and black bars are for warmed experimental field plots. Data are split between: growing season of May to September (left), and non-growing season of October to April (right).


Growing season
Non-growing season
Net Ecosystem Exchange (mg CO_2 m^{-2} hr^{-1})
200
0
-200
-400
-600
-800
-1000
-1200
-1400
Control vegetation
Shrub only
Graminoid only
Bryophyte only
Shrub & Graminoid
Shrub & Bryophyte
Graminoid & Bryophyte
No vegetation


Growing season
Non-growing season
Ecosystem Respiration (mg CO_2 m^{-2} hr^{-1})
800
600
400
200
0
Control vegetation
Shrub only
Graminoid only
Bryophyte only
Shrub & Graminoid
Shrub & Bryophyte
Graminoid & Bryophyte
No vegetation


Growing season
Non-growing season
N_2O flux (mg N_2O m^{-2} hr^{-1})
50
40
30
20
10
0
-10
-20
-30
-40
-50
Control vegetation
Shrub only
Graminoid only
Bryophyte only
Shrub & Graminoid
Shrub & Bryophyte
Graminoid & Bryophyte
No vegetation


Growing season
Non-growing season
CH4 Flux (mg CH4 m−2 hr−1)
1.8
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
Control vegetation
Shrub only
Graminoid only
Bryophyte only
Shrub & Graminoid
Shrub & Bryophyte
Graminoid & Bryophyte
No vegetation
Control vegetation
Shrub only
Graminoid only
Bryophyte only
Shrub & Graminoid
Shrub & Bryophyte
Graminoid & Bryophyte
No vegetation